NOTES ON THE METHODS OF FERTILISATION OF THE *GOODENIACEÆ.*

Part I.

By Alex. G. Hamilton.

(Plate xvi.)

The remarkable nature of the organs of fertilisation in this order appears to have early attracted the attention of botanists, and there are many allusions to them in works on Australian botany. With one or two exceptions to be noted presently, the early observations appear to have been made on dried specimens, a fact to be deplored, although not to be wondered at when we remember that much of the systematic work was done by English botanists, and that those who actually collected plants in Australia in the early days had such a wealth of new material to work out that they would scarcely have time or inclination to make long continued and close observations.

The earliest reference which I can find to the subject is by J. Sims in a description of *Goodenia grandiflora* (1), in which he gives an account of the process, evidently from observation of fresh specimens. This is in the main correct, but he makes the mistake of supposing that the pollen falls from the anthers into the cup instead of being packed, as described in a later paper by me (2). R. Brown has a reference to the subject in his "General Remarks on the Botany of Terra Australis" (3), pointing out that the flowers cannot be impregnated at the time of the bursting of the anthers, but that later on they may be, by the pollen of other flowers, or at a still later stage, by their own. It will be seen in the course of these notes that this is a correct conclusion. C.

Darwin, in a paper "On the Fertilisation of *Leschenaultia*" (4), gives a good account of the fertilisation of this genus from observation of living specimens of several species. This was followed by a "Note on the Stigmatic Apparatus of *Goodenoviæ*" by G. Bentham (5), which is a wonderful account of the process, when it is taken into consideration that the observations were for the most part, if not entirely, made on dried specimens. I shall notice his conclusions as to the different genera as I reach them in the course of my notes. H. Müller also describes the process, and takes the view that the plants of the order are solely cross-fertilised (6). In the Manual by R. Brown, Junr., there is an account of indusiate stigmas, in which is repeated the erroneous statement that the pollen falls into the cup and causes fertilisation (7). Some of the authors mentioned call upon Australian observers to work the subject out from fresh plants. So far as I am aware, there have been only two who have attempted this—Mr. E. Haviland, whose papers (8 and 9) I shall refer to under the genus *Goodenia*, and myself, in a paper already mentioned. Other papers on the nature and origin of the indusium by R. Brown (10 and 11), Bentham (12), and Lindley (13 and 14) I shall also have occasion to refer to.

In the present paper I propose to give the results of my observations of those species of *Scævola*, *Selliera*, and *Brunonia* which have come under my notice, and I shall continue in other instalments with other genera which I have had the opportunity of observing. I regret that I have had no opportunity of seeing living specimens of West Australian species, and tropical Australian species generally. I should be very grateful to any members who could send me seeds of such plants, especially of the genera *Leschenaultia*, *Diaspasis*, *Calogyne*, and *Anthotium*, for the purpose of cultivating them for observation, or failing seeds, dried flowering specimens.

1. Scævola suaveolens, R.Br.

In this species the five petals spread out like an open hand, the three centre petals lying quite flat, while the outer one on each side slants upwards and outwards from the plane of the others, so as to form guiding walls to the throat of the flower. The petals are bright blue with a greenish-yellow band from the mid-length in the median line. This yellow part in the three centre petals is thickly studded with brush-tipped hairs standing perpendicularly (Fig. 1); they are sticky and well adapted to catch pollen. The lateral petals have very few of these hairs. The flower buds are at first closely pressed to the stem of the plant by the leaves, from the axils of which they spring; but, as the flower progresses, each leaf bends downwards till at last it assumes a horizontal position, and in this movement it is followed by the flower, which is fully open when the horizontal position is reached. In the upper part of the plant, the flower develops before the leaf grows to any size, but even in this case the same movements are gone through, and the leaf, though perhaps smaller than the flower, still gives it support.

The flower is proterandrous. In the early buds, the style and indusium stand slightly higher than the anthers (Fig. 2), but as the bud matures, the anthers grow rapidly till they overtop the cup (Fig. 3) which is edged with stiff hairs. The style then grows upward through the anthers (Fig. 4), and at the same time these dehisce introrsely, and the brush of hairs on the margin of the cup clears the pollen out of them completely, the pollen dropping into the indusium (Fig. 5). This alternation of periods of growth between the style and the anthers is a remarkable feature, and occurs in all the species of the order so far as I am aware, but it appears to have been missed by observers prior to my paper (2) already referred to. The upward growth being very rapid, and the filaments being so elastic as to keep the anthers closely pressed to the cup, the pollen is pretty firmly packed, in which the pressure of the bud on the anthers also assists. The stigma at this stage is immature, at the bottom of the indusium (Fig. 6) and hidden by the grains of pollen. The edges of the cup now approach each other by a flattening of the indusium (Fig. 7), till at last the opening is a narrow slit fringed with hairs (Fig. 8). Up till this time, the style has lain horizontally in the bud, but now it bends upwards in the middle, and bursts the bud open on the upper side (Fig. 9), and at the same time the pollen begins to be forced through the slit at the mouth of the indusium by the growth of the stigma. I have noticed in some flowers that the mouth opens quickly and allows the pollen to drop out in a solid mass. The petals now expand, and by a further bending of the style, the mouth of the cup rests upon and in contact with the brush-tipped hairs on the petals. During this period, the leaf from the axil of which the flower springs, reaches the horizontal position, and when the flower is fully open it is spread out on the leaf which forms a platform on which insects visiting the flower can alight. I have not observed this correlation of movements and growth between the leaf and flower in any other member of the order. When the flower is fully open, the stigma continues to grow outward from the bottom of the indusium, and forces a constant shower of pollen between the hairs at the mouth, which falls on the brush-like hairs on the petals. Any insect visiting the flower is guided in the right direction by the lateral petals, the convergence of the central petals, and the guiding lines of colour; to reach the throat of the flower it has to force itself under the pollen-shedding cup, and in doing this it is dusted with pollen on the dorsal surface by the cup, and on the ventral surface by the brushes on the petals.

Before the stigma has grown so much as to project from the opening of the indusium, the flower withers, the lateral petals a considerable time before the central ones, and the supporting leaf, by a twisting of the leaf-stalk, moves round so as to be above the flower, and then turns on one side and conceals it. It is during this movement, and after it is complete, that the stigma first emerges from the indusium (Fig. 9). It is difficult to give any reason for this concealment, as it is just at the stage when insects would begin to be useful to the plant by placing pollen from other flowers on the stigma, that concealment begins. The withering, too, seems to indicate that the plant no longer requires the aid of insects. But there is evidence that insects do visit these withered and concealed flowers, for if a series of stigmata from them be examined, most of them will be found to have moth scales adhering to them in addition to pollen and fragments of brush-like hairs. It would appear then that the visiting insects carry pollen from those flowers which are distributing it from the indusium, both on their upper and under surfaces, and in visiting other flowers, leave it either on the brush-tipped hairs whence it is taken up by the mature stigma resting on these, or on the stigma itself from their backs, and in this way cross-fertilisation is ensured. But it is not necessary for ensuring cross-fertilisation, that the concealed flowers should be visited, if when in the pollen-distributing stage they have been freely visited. For each insect not only takes pollen from an open flower, but if it has visited another, it also leaves some on the brushes, and as the stigma when it emerges from the indusium rests on these, it would find there the pollen necessary for impregnation. If the flowers should not be at all visited, they are very likely to be self-fertilised by the pollen which dropped on the brushes. In fact, even if insect-visited it would seem as if they were certain to be partly self-fertilised unless what has been shown to be the case with other plants obtains here, viz., that the foreign pollen is prepotent. In G. Bentham's account of the stigmatic apparatus in this order (5), he says—" In *Scævola* . . . . the stigma is small and more buried in it" [the indusium]. This I have not found to be the case. In fact, in the species I have examined, I have found the stigma to project very much—more so than in most other genera.

By cutting away the indusium from the mature stigma, pollen may be found inside the cup, being forced into the crevices behind the stigma by the packing process. But it is not at all likely that the base of the stigma is functional and capable of being fertilised, and I have never observed pollen-tubes emitted by the pollen in this situation. The plant fruits very freely, and, as the specific name denotes, the flower is sweet-scented. The leaves, stem and calyx are closely covered with stiff hairs, lying close to the surface, which give the plant a harsh feel, and which may be for the purpose of keeping away creeping insects, but they appear to me to lie too flat to be of service in this way.

2. Scævola hispida, Cav.

The flower spreads out rather flatly, the lateral petals being twisted so as to form guides to the tube of the flower, and there are guiding lines of yellowish-green on the petals, which latter are bright purple. The centre petals vary as to smoothness, being sometimes glabrous, sometimes with lines of soft hairs, or again having raised thin jagged ridges, passing into forked hairs in the throat of the flower (Fig. 11). The indusium when young and open is 4-angled at the mouth (Fig. 12), and has the fringe of stiff hairs which aid in brushing the pollen out of the dehiscing anthers. The method of packing the pollen into the indusium is as in the preceding species. The pollen is packed before the flower opens, and is driven out before the up-growing stigma. The style arches over so as to bring the mouth of the cup down upon the centre petals (Fig. 13). Insects visiting the flower and inserting their probosces into the tube are therefore dusted with pollen. Contrary to what occurs in *S. suaveolens*, the flower does not wither before the out growth of the stigma. This last grows out in a crescent shape so as to leave a passage between for insects (Fig. 13), and at the same time the horns can take up pollen adhering to an insect after a previous visit to a pollen-shedding flower. And the ridges and hairs of the petals, while not so effective as those of *S. suaveolens*, are yet capable of holding pollen received from the ventral side of an insect, which the stigma would then take up. The plant has the power of self-fertilisation as in the preceding species, as its own pollen lies in quantities on the hairs of the petals, and if not removed by insects, comes in contact with the stigma when that organ protrudes. In fact, it is certain that some of the plant's own pollen must reach the stigma. There is no scent, and I failed to detect nectar in the tube, but there is some attraction for insects, as they frequently visit the flowers.

3. Scævola Hookeri, F.v.M.

This species differs from the preceding two in having no hairs on the margin of the indusium, but the pollen is collected as in the others, and all the rest of the process is similar. The outgrown stigma is remarkable for its large size. In this and the other species, as indeed in most of the order, there are quantities of light stiff hairs on the style and outer sides of the cup. Their purpose is probably to prevent small insects getting at the pollen by a path which would not ensure the placing of pollen on the stigma. The whole of this plant is slightly hairy, and as it is a prostrate plant, it is perhaps for the same purpose that it is hairy.

4. Selliera radicans, Cav.

The flowers are less flattened than in *Scævola*, and assume a bell-shape, slit down one side. The process of pollen-packing is the same. The hairs on the lip of the indusium are remarkably few, and very thick and strong as compared with any other member of the order which I have seen (Fig. 14, *a*). They cannot act as a brush in taking the pollen out of the anthers, but they bend over the closed mouth of the indusium and form a grille, through which the pollen is strained (Fig. 14, *b*). The cup is hairy outside (Fig. 14) and these hairs are also much stronger; they are most plentiful on the lower side; pollen is frequently entangled in them. There are usually a number of small intensely black spots on the outside of the indusium, which may be a fungoid disease. The stigma grows out very largely (Fig. 15), and bends over at the corners (Figs. 16 and 17), a feature found in *Velleya* and at least in one *Goodenia*. There is no scent; the flowers are greenish, and secrete much nectar. The plants bear fruit very freely.

5. Brunonia australis, Sm.

In this species I met with a number of unusual features, which perhaps might have been expected considering the numerous affinities of the plant with orders outside the *Goodeniaceæ*. R. Brown advocated making a separate order of it (11), pointing out its many features of resemblance and difference when compared with the orders *Compositæ*, *Goodeniaceæ*, and *Campanulaceæ*, and concluding that its proper place in the natural system was between *Compositæ* and *Goodeniaceæ*. He also speculates on the origin of the indusium, and from a consideration of the order *Stylideæ* in connection with *Brunonia*, is disposed to think that it consists of a series of modified stamina.

The flowers grow in a head which bears a considerable resemblance to *Scabiosa*—a fact that is patent to the ordinary observer, as is evidenced by its bearing the common name of "Bachelor's buttons," which is also applied to *Scabiosa*. Indeed, Sir James Smith was disposed to refer it to the order *Dipsaceæ*. The colour is white, pink or pale blue. The anthers are connate as in *Dampiera* and *Leschenaultia*, and are sometimes emptied in the usual way by the upgrowing indusium. But in the same head of flowers I frequently found some indusia full of pollen, and closed by the accurate contact of the lips, which are destitute of the hairy fringe, but thickened (Fig. 18); and others in which, although the flower was open, the style and indusium had grown up above the anthers, which were still closed and full. The indusium in this case was so widely opened that the stigma could be seen at the bottom. Again, in others the flowers were withered, but the stigma not grown out, and the indusium was open and full of pollen. A few were found with the indusia closed and quite free from pollen, and the stigma not grown out (Fig. 19). Others again had the stigma grown out (Fig. 20) and either plentifully smeared with pollen or quite free from it, the styles being withered, brown, and on the point of dropping off. Packed indusia and outgrown stigmata were the exception; empty indusia and ungrown stigmata the rule.

I am at a loss to account for such an anomalous condition in this plant, unless it be that there is less necessity for the collecting of pollen and doling it out a little at a time to visiting insects, on account of the flowers being compacted into a head; but it would be necessary in that case that the stigmata should grow out freely, and that is not common, so far as my experience goes. It may perhaps be that, being a link between so many orders, the characters pertaining to the *Goodeniaceæ* have not become fully fixed, and that the plant is, so to speak, in a plastic condition.

The indusium is bilabiate in *Brunonia*, as in *Selliera* (Figs. 14 and 18), the outside of the style is glandular and has gland-tipped hairs all round for half its length upwards, and a few stiff hairs grow on the outside of the indusium. The stigma grows out transversely to the mouth (Fig. 20), in which it differs from all other plants of the order which I have examined.

The conclusion I have arrived at with regard to the first four plants is, that the contrivances all point to cross-fertilisation by insects, but that in case of that failing, the same contrivances secure fertilisation by the plant's own pollen.

It is interesting to compare the methods of distributing the pollen in the three natural orders, *Lobeliaceæ*, *Goodeniaceæ*, and *Campanulaceæ*. In the first, the anthers surround the style closely, and as that organ grows upwards, it pushes the pollen before it, so that it issues in a stream from the orifice of the tube formed by the anthers. In the second order, the open indusium, pushed up between the anthers by the growth of the style, brushes the pollen into itself, and then closing, the outgrowth of the enclosed stigma forces the pollen out gradually. In the last, the anthers are closely adpressed to the style, and wither, leaving their pollen adhering to it in a uniformly thick coat; the pollen is then set free by the drying up of the sticky glands on the style, to which it adhered, and is carried off by insects which visit the flower in search of nectar and pollen. These very different methods of securing the same end are all the result of modifications of the same organs.

I am inclined to think that the study of this subject throws some light on the descent of the order *Goodeniaceæ*. I take *Scævola* to be the ancestral form, or the nearest to it, on account of its manifestly simpler arrangements for fertilisation; and this view I think supported by the fact that *Scævola* is the only genus of the order which is very widely distributed, being found in Australia, New Zealand, several Pacific islands, Asia, Africa, South America, and the West Indies.

C. Darwin has pointed out that a very wide distribution probably indicates a very ancient origin. I hope to be able to discuss this subject in another paper.

I have to thank Dr. Maxwell T. Masters, Editor of the "Gardeners' Chronicle," for a manuscript copy of C. Darwin's very interesting account of *Leschenaultia*, which I could not find in any Sydney library. Mr. C. Moore and Mr. C. Musson, too, very kindly gave me specimens of a number of plants of the order which I had not previously seen.

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(13) Lindley, J. "Nature of Indusium in *Goodeniaceæ*," "Vegetable Kingdom," p. 694.

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Postscript (July 3rd, 1894) :—The quite recent addition to the Society's library of some of the earlier volumes of the Proceedings and Transactions of the New Zealand Institute—wanting since the destruction of the library in 1882—has enabled Mr. J. J. Fletcher to call my attention to an important paper* by Mr. Cheeseman, on the fertilisation of *Selliera*, of which I was previously unaware, and which I regret that I was unable to refer to in the proper place. The author's observations (made in 1876) agree with mine, except in some minor details which arise from slight structural differences. For example, he describes the hairs on the margin of the indusium, and the outside, as few and weak, whereas I have always observed them to be stiffer than in others of the order. He believes the functions of the hairs to be to catch the pollen and detain it on the outside of the indusium. But examination of many species of the order leads me to think that the marginal cilia are, first, intended to brush the pollen out of the anthers as the style lengthens ; and second, to strain it out a little at a time as the stigma grows outward. The function of the hairs on the upper surface of the indusium I think is to protect the pollen

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* On the Fertilisation of *Selliera*. By T. F. Cheeseman, F.L.S., Proc. and Trans. of N.Z. Inst. Vol. ix, p. 542.

from dew, but I shall enter into this more fully in another contribution. Mr. Cheeseman gives a most interesting account of the visits of insects to the flowers. He finds that the most frequent visitors are Diptera, but Hymenoptera, including the hive-bee, and ants also frequent the flowers, as does a day-flying moth, *Leptosoma annulatum*.

EXPLANATION OF PLATE XVI.

Scævola suaveolens.

Fig. 1.—Brush-like hairs on petals.
Fig. 2.—Anthers and indusium in early bud.
Fig. 3.—Anthers in advanced bud ready to dehisce.
Fig. 4.—Style grown up and anthers emptied of pollen.
Fig. 5.—Cup full of pollen before closing.
Fig. 6.—Indusium cut open, showing immature stigma at the bottom.
Fig. 7.—Indusium closed on pollen.
Fig. 8.—Mouth of closed indusium, showing strainer of hairs.
Fig. 9.—Bud bursting from bending of style.
Fig. 10.—Stigma outgrown from indusium.

Scævola hispida.

Fig. 11.—Ridges and hairs on petals.
Fig. 12.—Indusium, showing 4-angled shape.
Fig. 13.—Position of indusium and mature stigma in flower.

Selliera radicans.

Fig. 14.—*a*, Indusium showing hairs on margin; *b*, closed, showing strainer of hairs.
Fig. 15.—Stigma outgrown.
Fig. 16.—Stigma outgrown, with corners bent down; from below.
Fig. 17.—Stigma outgrown, with corners bent down; from side.

Brunonia australis.

Fig. 18.—Open indusium, showing rib round mouth.
Fig. 19.—Indusium closed.
Fig. 20.—Indusium with outgrown stigma.